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Key Points:
- Sea ice can be net heterotrophic during the Arctic spring, despite sufficient light being available for photosynthesis
- A rapid (within 1 week) switch from net heterotrophy to autotrophy coincided with a transition in the algal community from pennate to centric diatoms
- The potential for heterotrophy during the spring bloom highlights a complexity of carbon cycling in sea ice not previously anticipated

Supporting Information:
- Supporting Information S1

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Net community production in the bottom of first-year sea ice over the Arctic spring bloom

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Abstract The balance of photosynthesis and respiration by organisms like algae and bacteria determines whether sea ice is net heterotrophic or autotrophic. In turn this clarifies the influence of microbes on atmosphere-ice-ocean gas fluxes and their contribution to the trophic system. In this study we define two phases of the spring bloom based on bottom ice net community production and algal growth. Phase I was characterized by limited algal accumulation and low productivity, which at times resulted in net heterotrophy. Greater productivity in Phase II drove rapid algal accumulation that consistently produced net autotrophic conditions. The different phases were associated with seasonal shifts in light availability and species dominance. Results from this study demonstrate the importance of community respiration on spring productivity, as respiration rates can maintain a heterotrophic state independent of algal growth. This challenges previous assumptions of a fully autotrophic sea ice community during the ice-covered spring.

1. Introduction

Autotrophic protists and heterotrophic bacteria dominate the microbial communities of sea ice, inhabiting brine inclusions and the surfaces of ice crystals, principally at the ice-water interface [*Legendre et al*., 1992; *Deming*, 2010]. In addition to brine and meltwater dynamics [*Glud et al*., 2002], the photosynthetic and respiratory activities of these organisms regulate the concentration of O_2 in sea ice [*Søgaard et al*., 2010]. The overall difference between photosynthesis and respiration represents net community production and describes whether sea ice may be considered as a net autotrophic (O_2 gain) or heterotrophic (O_2 loss) system [*Codispoti et al*., 2013]. The productive state of the biological community affects gas fluxes between the ice and ocean [*Brown et al*., 2015], as well as carbon cycling within the Arctic marine system [*Matrai and Apollonio*, 2013; *Michel et al*., 2015].

Absent or limited availability of light through the Arctic winter and early spring prevents or restricts photosynthesis and instead favors bacteria and protist heterotrophy [*Riedel et al*., 2007, 2008]. However, a seasonal increase in downwelling irradiance during spring initiates a bloom that is typically characterized by the rapid growth and increased production of autotrophic protists (algae) in the bottom portion of the sea ice [*Leu et al*., 2015]. The temporal shift in microbial composition and productivity affects the balance of O_2 losses and gains, which can result in the bottom layer of ice transitioning from an overall state of net equilibrium or heterotrophy prior to the ice algal bloom, to a state of autotrophy once the bloom commences [*Søgaard et al*., 2010]. Heterotrophic processes may once again dominate the bottom ice with the bloom's decline and following its termination [*Kaartokallio*, 2004]. Other factors potentially affecting respiration and photosynthesis include temperature [*Arrigo and Sullivan*, 1992; *Kirchmann*, 2008], nutrient availability [*Gosselin et al*., 1990; *Kaartokallio et al*., 2013], and algal species composition [*Campbell et al*., 2017]. However, estimates of sea ice net community production are relatively sparse [e.g., *Rysgaard et al*., 2008; *Nguyen and Maranger*, 2011; *Glud et al*., 2014], and it is not well understood how changing environmental conditions influence net community production throughout the spring algal bloom. It is important to improve our understanding of the mechanisms controlling net community production for predicting the response of sea ice communities to climate-induced changes, such as greater light availability under a potentially thinner future snow cover [*Webster et al*., 2014].

As part of the 2014 Ice Covered Ecosystem-CAMbridge bay Process Study we assessed the potential for net heterotrophy during the ice algal bloom by recording net community production of bottom first-year sea ice

for approximately 7 weeks in the spring. We define the productive state of the bottom layer of sea ice based on these measurements and evaluate its seasonal progression.

2. Data Collection and Processing

Samples were collected on 12 occasions between 21 April and 9 June 2014 from landfast first-year sea ice in Dease Strait (69°1′N, 105°19′W), near Cambridge Bay, Nunavut, Canada. Sites with <0.1 m snow cover (relatively high light availability) were sampled approximately every 4 days over the spring. During each sampling event the bottom 0.05 m of six to eight ice cores were pooled and melted in filtered seawater to determine concentrations of chlorophyll *a* (chl *a*) and particulate organic carbon (POC) [*Campbell et al*., 2016] and taxonomic composition of the algal community [*Campbell et al*., 2017] (see supporting information Text S1). All reported measurements of abundance and productivity (described below) have been corrected for the filtered seawater dilution.

Net community production was calculated as the change in oxygen over time, relative to the concentration of oxygen at time zero (μmol O_2 l^{-1} h^{-1}). It was determined by incubating aliquots of the melted ice sample in bottles equipped with oxygen optodes according to *Campbell et al*. [2016], under conditions of darkness and at scalar light intensities of approximately 10, 21, and 55 μmol m^{-2} s^{-1}. These light intensities were determined by averaging measurements made in each sample-filled bottle prior to all incubations and will be used hereafter when referencing incubation light levels (see supporting information Text S2). We note that subsamples were not filtered prior to incubation; however, grazers (meiofauna, ciliates, and metazoan larvae) were not documented during microscopy analysis of the pooled core samples [*Campbell et al*., 2017]. Therefore, their influence on net community production estimates was assumed minimal. Net community production at the different incubation light intensities was modeled using the exponential equation of *Platt et al*. [1980] modified by *Arrigo et al*. [2010] that excludes photoinhibition, as this was not observed at our incubation light intensities. The exponential model was used to estimate the scalar irradiance (μmol m^{-2} s^{-1}) at which net community production was equivalent to zero, which we define as the light compensation point of the bottom ice community (C_{IC}). We differentiate this from the light compensation point (I_c) that is typically defined in modeling of photosynthesis-irradiance curves, as I_c represents the scalar irradiance when gross primary production rather than net community production is zero.

Hourly estimates of scalar irradiance averaged for the bottom ice algal layer were calculated using two different methods, to provide lower and upper theoretical limits on the quantity of light absorbed by algal cells. Through method (1) the lower bound ($\bar{E}_0$) was estimated by assuming constant exponential attenuation of light across a 0.025 m algal layer, according to parameterizations presented in *Ehn and Mundy* [2013]. This parameterization was originally derived from estimates of downwelling photosynthetically active radiation (PAR) transmitted to the ice-water interface as well as chlorophyll *a* concentrations at the base of the ice (see supporting information Text S3). Transmittance was calculated relative to measurements of PAR at the snow surface. Through method (2) the upper bound of the scalar irradiance ($\hat{E}_0$) was derived from the principle of energy conservation via Gershun's equation, again calculated using parameterizations provided in *Ehn and Mundy* [2013]. This second method accounts for multiple scattering of light within the algal layer, which increases nonlinearly as a function of chlorophyll *a*. By directly accounting for the effects of multiple scattering, $\hat{E}_0$ is always greater than $\bar{E}_0$ in sea ice [*Ehn and Mundy*, 2013].

Hourly variations of in situ net community production were estimated for days of ice core collection by solving the exponential model described above at in situ scalar irradiances. Hourly estimates of net community production from $\bar{E}_0$ or $\hat{E}_0$ were then integrated over the 24 h diurnal period, giving net community production over the full diurnal cycle.

3. The ice Algal Community

Ice algae were present in the region prior to the start of the study, with chl *a* and POC concentrations between 7 and 15 March averaging (±SD) 1.2 ± 1.2 and 53.4 ± 21.1 mg m^{-2}, respectively. These estimates were considerably lower than concentrations in Figure 1, indicating positive accumulation, with conservative daily net production rate estimates (reported hereafter with standard errors) on the order of 0.12 ± 0.02 mg chl *a* m^{-2} d^{-1} and 8.89 ± 1.43 mg C m^{-2} d^{-1} during early spring (8 March to 21 April). Chlorophyll *a* and POC

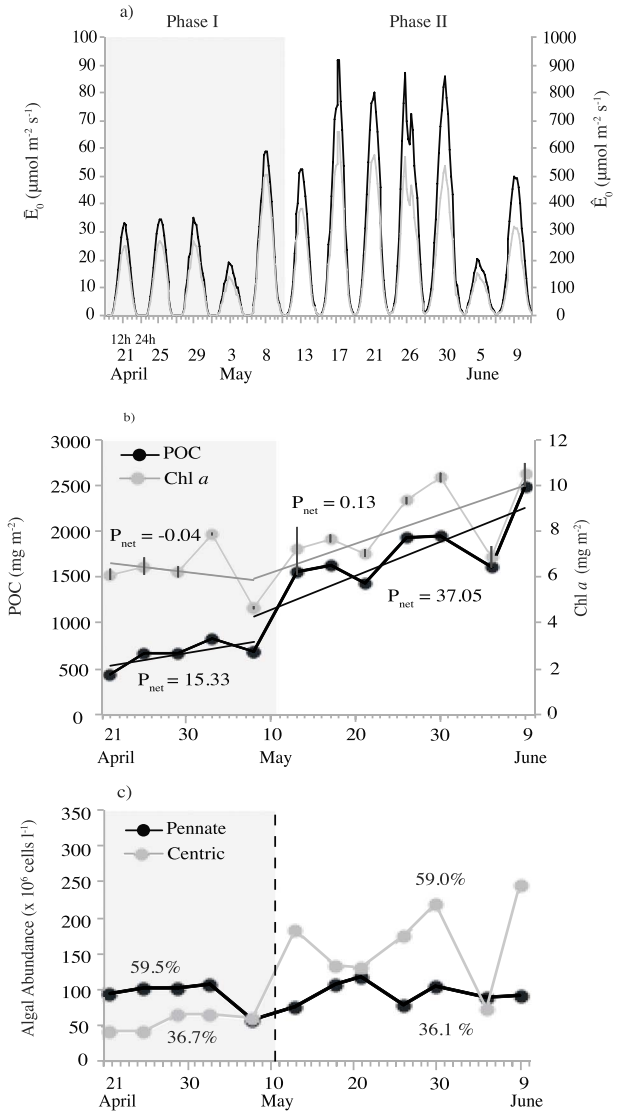

Figure 1. (a) ($\bar{E}_0$) (gray) and ($\hat{E}_0$) (black) for days of ice core collection, (b) seasonal concentration of bottom ice particulate organic carbon (POC) and chlorophyll *a* (chl *a*) (mean ± SD) with linear trend lines and daily net production rates (P_{net}) (mg m^{-2} d^{-1}) before and after 8 May, and (c) abundance of pennate and centric diatoms in the ice algal community over the spring during Phases I (gray) and II (white). The dashed line in Figure 1c highlights the approximate division between pennate and centric diatom dominance in the bottom ice community, where the specific percent abundance of each taxonomic group relative to the entire bottom ice community is reported for each phase.

accumulated in the bottom ice from April to June, following a seasonal increase in light availability [*Campbell et al.*, 2016]. This is with the exception of a small decrease in measurements after the snowstorm event on 3 June, likely as a result of reduced light availability from the freshly deposited snow cover that had a greater surface albedo [*Campbell et al.*, 2016]. Overall, the rates of accumulation were not constant and the study period can be roughly divided into two phases, particularly surrounding a jump in POC between 8 and 13 May (Figure 1).

The seasonal daily net production rates for this 21 April to 9 June study period were 0.07 ± 0.03 mg m^{-2} d^{-1} for chl *a* and 37.14 ± 4.76 mg m^{-2} d^{-1} for POC. However, in Phase I from 21 April to 8 May, chl *a* accumulation was nearly zero (−0.04 ± 0.10 mg m^{-2} d^{-1}) and POC accumulation was approximately 2.5 times lower (15.33 ± 8.80 mg m^{-2} d^{-1}) than the overall trend (Figure 1). Phase II from 8 May to 5 June was characterized by significantly greater chl *a* ($p < 0.05$) and POC ($p < 0.05$) (see supporting information Table S1). This was linked to 85% higher daily net production rates for chl *a* (0.13 ± 0.05 mg m^{-2} d^{-1}) and nearly equivalent daily net production rates for POC (37.05 ± 11.04 mg m^{-2} d^{-1}), relative to seasonal trends. Excluding estimates between 8 and 13 May from this comparison of Phase II daily net production rates, seasonal trends of chl *a* (0.09 ± 0.06 mg m^{-2} d^{-1}) and POC (25.17 ± 11.5 mg m^{-2} d^{-1}) are still greater than in Phase I.

Daily averaged $\bar{E}_0$ ($\bar{E}_{0(daily)}$) and $\hat{E}_0$ ($\hat{E}_{0(daily)}$) were also greater in Phase II ($p < 0.10$). We note that the difference in scalar irradiance between phases had greater significance ($p < 0.05$) when outliers from 5 and 9 June sample dates were excluded from analysis. A late-season snowstorm on 3 June caused a large drop in PAR transmittance that resulted in unseasonably low $\bar{E}_0$ and $\hat{E}_0$ estimates for subsequent measurements.

Diatoms dominated the algal community during both growth phases, particularly the pennate diatom *Nitzschia frigida* and centric diatoms of the genus *Attheya*. However, an unexpected increase in abundance of centric forms over the spring shifted the composition of the ice algal community from dominant pennates to dominant centrics after 8 May (i.e., between Phases I and II) (Figure 1c). The transition to a significantly greater ($p < 0.05$) abundance of centric diatoms in Phase II (see supporting information Table S1) primarily drove the seasonal trends in chl *a* and POC (Figure 1b). It was likely a result of centric diatoms

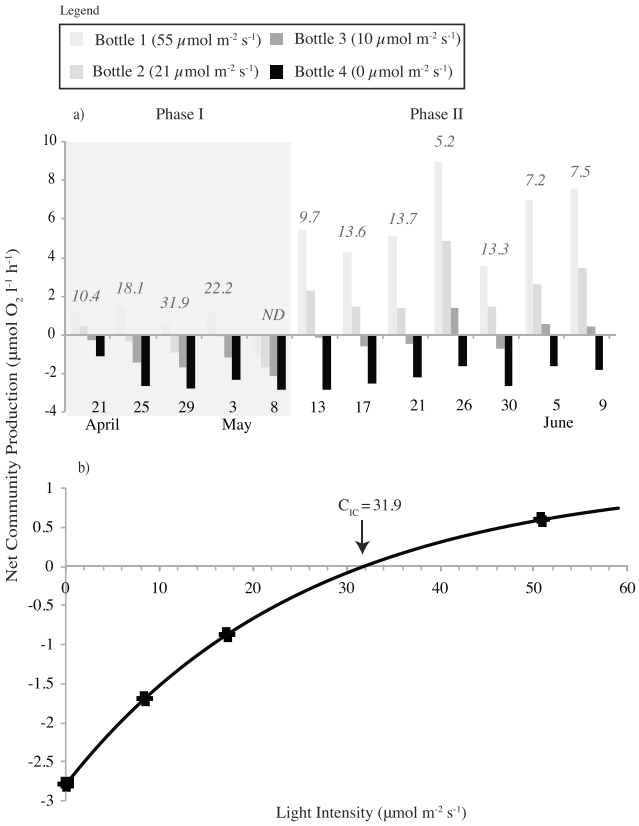

Figure 2. (a) Net community production of bottom ice samples (0.05 m) incubated at light intensities of approximately 0, 10, 21, and 55 μmol m^{-2} s^{-1} during Phases I (gray) and II (white) and (b) an exponential model of net community production on 29 April to highlight the community light compensation point (C_{IC}) parameter. In Figure 2a, values of C_{IC} (μmol m^{-2} s^{-1}) calculated for all incubations are listed above the respective production estimates, expect for 8 May where it was not defined (ND).

outcompeting pennates in the low-nitrogen and low-salinity conditions of the study region (see supporting information Table S1), as transmitted PAR increased and became less limiting [see *Campbell et al.*, 2017]. Greater tolerance of centric diatoms to these conditions has been documented previously and is described in detail by *Campbell et al.* [2017, and references therein].

4. Optode-Derived Measurements of Net Community Production

The net community production of samples incubated under the various light intensities and in darkness is shown in Figure 2. Illuminated estimates were far below maximum rates of sea ice net community production reported by *Suzuki et al.* [1997] that were on the order of 50–190 μmol O_2 l^{-1} h^{-1} but were comparable to incubation estimates with similar light conditions once differences in biomass have been accounted for [*Rysgaard et al.*, 2008; *Søgaard et al.*, 2010]. Although estimates of net community production in darkness can vary considerably, the average estimate of oxygen uptake in this study at 2.2 ± 0.6 μmol O_2 l^{-1} h^{-1} was within the lower range documented for Arctic sea ice of 0.04–93.8 μmol O_2 l^{-1} h^{-1} [*Suzuki et al.*, 1997; *Nguyen and Maranger*, 2011]. Furthermore, dark respiration contributed 30% of gross primary production [*Campbell et al.*, 2016], which is similar to previous estimates of between 10 and 41% [*Falkowski and Owens*, 1978; *Suzuki et al.*, 1997].

In all incubations the production of oxygen increased or consumption was reduced with scalar irradiance, due to the contribution of algal photosynthesis exceeding that of community respiration. However, during Phase I hourly net community production was considerably lower than during Phase II (see supporting information Table S1). This corresponded to significantly higher C_{IC} estimates (see supporting information Table S1) in Phase I, meaning that on average 100% higher scalar irradiance was required to create positive net production in the bottom ice community at this time. Photoacclimation cannot account for the observed difference in C_{IC} between phases, as the compensation light intensity (I_C) of individual cells did not significantly change over the spring [*Campbell et al.*, 2016].

5. Seasonal Changes in Net Community Production

There is uncertainty associated with estimating light available to algae living in the bottom ice due to measurement error, as well as the effects of multiple scattering and self-shading within the algal layer [*Ehn and Mundy*, 2013]. As a result, our estimates of daily net community production represent approximations of the productive state in bottom sea ice. In an effort to characterize the potential range of daily net community production, we present estimates calculated from both $\bar{E}_0$ and $\hat{E}_0$ (Figure 3), as the average intensity of $\hat{E}_0$ was

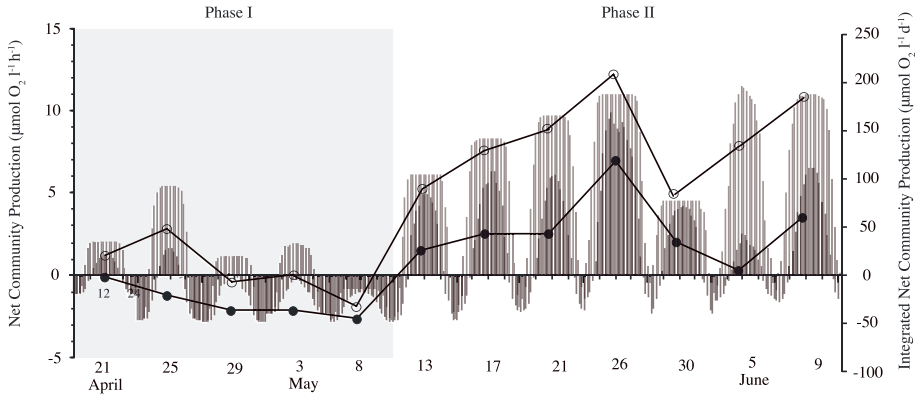

Figure 3. Net community production in the bottom ice samples (0.05 m) modeled over 24 h on core collection days, using $\bar{E}_0$ (dark gray) or $\hat{E}_0$ (light gray) during Phases I (gray) and II (white). Circles indicate daily integrated estimates of net community production modeled from $\bar{E}_0$ (black) and $\hat{E}_0$ (hollow), respectively.

around 7 times greater than $\bar{E}_0$. It follows that net community production calculated from $\bar{E}_0$ approximates a lower limit, while those calculated from $\hat{E}_0$ represent the upper theoretical limit.

There is a clear difference in daily integrated net community production between Phases I and II (Figure 3). Between 21 April and 8 May net community production calculated from $\bar{E}_0$ was negative (oxygen was consumed in the sea ice) and average production over 24 h was −27.9 μmol O_2 l^{-1} h^{-1} (−1394 μmol O_2 m^{-2} h^{-1}). In comparison, net community production calculated from $\bar{E}_0$ after 8 May was consistently positive (oxygen was produced in the sea ice more than it was consumed) and average production over 24 h at 47.3 μmol O_2 l^{-1} h^{-1} (2364 μmol O_2 m^{-2} h^{-1}) was significantly greater (see supporting information Table S1). It follows that based on $\bar{E}_0$ and the influence of biology alone (i.e., excluding contributions from brine or meltwater drainage) the bottom ice can be classified as net heterotrophic during growth Phase I (21 April to 8 May), before transitioning into a net autotrophic system in Phase II (13 May to 9 June). Although, we note that hourly net community production based on $\bar{E}_0$ remained heterotrophic for a portion of the nighttime throughout the spring, with net oxygen consumption occurring for 19 ± 5 h in Phase I and 9 ± 2 h in Phase II.

Our findings support previous observations by *Rysgaard and Glud* [2004] and *Rysgaard et al.* [2008] that net heterotrophy can occur in the presence of primary production in sea ice. However, to our knowledge we report the first observations of a strong shift in the productive state of sea ice over the bloom period. The potential for heterotrophic conditions during the ice algal bloom indicates that algal photosynthesis does not necessarily create a sink for CO_2 [e.g., *Delille et al.*, 2007]. Instead, the role of sea ice in the biological pump is likely more complex and depends on the seasonally evolving balance between community photosynthesis and respiration.

Estimates for the higher scalar irradiance ($\hat{E}_0$)-based net community production were also significantly greater during Phase II than Phase I (see supporting information Table S1), and they highlight a transition from low to high productive states between 8 and 13 May. However, the average daily productivity based on $\hat{E}_0$ was nearly 3 times greater than estimations from $\bar{E}_0$, which resulted in heterotrophic (negative) estimates for only two of five sampling days during Phase I (Figure 3). Nevertheless, these observations support the potential for net heterotrophy to occur during periods of moderate carbon biomass accumulation in the bottom ice, in spite of relatively high PAR availability (Figure 1). We note that the potential for heterotrophic conditions is likely to decrease with carbon accumulation, as net community production calculated from either $\bar{E}_0$ (r = 0.80) or $\hat{E}_0$ (r = 0.86) is significantly ($p < 0.05$) and positively correlated with POC over the study period.

The seasonal increase in net community production and associated higher net community production during Phase II (see supporting information Table S1) are in part driven by increasing scalar irradiance throughout the spring (Figure 1a). However, the rapid shift in net community production between 8 and 13 May did not directly correspond to a rapid change in scalar irradiance (Figure 1a) or a reduction in the rate of oxygen uptake in the dark bottle (Figure 2a). Instead, it paralleled the equally rapid shift in community composition

from a majority of pennate to centric diatoms (Figure 1c). The influence of diatom abundance is further supported by significant ($p < 0.05$) linear correlations of numerical centric abundance with net community production based on $\bar{E}_0$ ($r = 0.74$) and $\hat{E}_0$ ($r = 0.67$), respectively. We note that temperature and the concentration of nitrate and nitrite in the bottom ice did not directly affect net community production variability, as these variables were not significantly different between phases (see supporting information Table S1) and were not correlated with $\bar{E}_0$ or $\hat{E}_0$-based production over the spring (data not shown). Although, low-nitrogen conditions in the region likely affected net community production indirectly by facilitating growth of the smaller centric diatoms in the ice, which contributed to the observed shift in species dominance [see *Campbell et al.*, 2017].

6. Early Spring Biomass Accumulation Under Net Heterotrophic Conditions

It is notable that POC increased slowly during Phase I, even though the bottom ice community was principally net heterotrophic (Figures 1b and 3). Accumulation of POC could have been possible during this period (i) if nonalgal respiration exceeded photosynthetic production of oxygen, (ii) under conditions of facultative heterotrophy, and/or (iii) if there was an allochthonous supply of biomass to the ice.

Heterotrophic bacteria typically exhibit the greatest influence on community respiration in sea ice [*Deming*, 2010; *Nguyen and Maranger*, 2011]. However, in this study, ^{3}H-leucine incubations of the bottom ice was low at 0.02 to 0.38 μg C l^{-1} h^{-1} [see *Campbell et al.*, 2017]. Even when combined with bacterial respiration estimated using a bacterial growth efficiency of 0.186 [*Nguyen et al.*, 2012], heterotrophic bacteria only accounted for <7.5% of oxygen consumption in the dark incubation bottles. This emphasizes that bacteria were not responsible for the productive state in Phase I. Moreover, bacterial production and net community production in the dark were not significantly different between Phases I and II (see supporting information Table S1), indicating that variability in algal or bacterial respiration was not the cause of the seasonal shift in productive state.

We note the potential for bacterial biomass to contribute to POC in the bottom ice, particularly following the possible stimulation of bacterial production with supply of dissolved organic carbon (DOC) substrate from the water column [*Thomas et al.*, 2001]. However, low estimates of bacterial production, and a lack of association between DOC at the ice-water interface (averaging 1.8 ± 0.06 mg C l^{-1}, data not shown) and bacterial production, indicate that this contribution was minimal during our study [*Campbell et al.*, 2017].

During periods of darkness or low light limitation, diatoms can continue metabolism through heterotrophic uptake of dissolved or particulate organic carbon (facultative heterotrophy) that includes exopolymeric substances (EPS) previously released [*Palmisano and Sullivan*, 1982; *Zhang et al.*, 1998; *Tuchman et al.*, 2006; *Niemi et al.*, 2011]. Although this strategy has not been directly observed in nature, facultative heterotrophy of DOC by sea ice algae could have contributed to the increase of POC during heterotrophic conditions.

Incorporation of algae into sea ice by sieving cells from the water column is one possible colonization mechanism during initial ice formation [*Syvertsen*, 1991; *Spindler*, 1994; *Różańska et al.*, 2008]. Further attachment of pelagic cells may also occur during lamellar ice growth [*Spindler*, 1994; *Lund-Hansen et al.*, 2016], a process that is aided by the production of EPS by many algae [*Różańska et al.*, 2008; *Krembs et al.*, 2011]. We speculate that this latter mechanism of cell colonization at the growth interface contributed to the moderate increase in POC documented in Phase I (Figure 1), where cells were slowly concentrated from the sparsely populated water column that had average chl *a* concentrations of only 0.24 μg l^{-1} at 5 m depth over the spring. This mechanism of allochthonous biomass supply is further supported by ice growth measured over the entire sampling period [*Campbell et al.*, 2017] and the regular occurrence of dominant ice species *Nitzschia frigida* and *Attheya* spp. (both >4 μm) in the water column. It also aligns with previous hypotheses that biomass accumulation via pelagic colonization of sea ice may exceed in situ growth [*Krembs et al.*, 2000, 2002], if algal productivity is low. Although significant pelagic colonization would also drive increases in chl *a*, it was not observed (Figure 1).

We note that vertical transport of POC to the bottom ice from higher up in the ice profile, via brine drainage, was not significant [*Lund-Hansen et al.*, 2014; *Aumack et al.*, 2014], as concentrations of POC and chl *a* from 0.05 to 0.1 m in the ice remained constant or even increased during Phase I. Increased grazing pressure at the ice-water interface and the resultant products of sloppy feeding could also have contributed to POC

accumulation during Phase I, particularly if pelagic grazers (e.g., zooplankton) preferred the pennate forms of algae dominant before 13 May. Unfortunately, grazing pressure was not assessed in this research to confirm this hypothesis.

7. Summary

This study shows the potential for net heterotrophic conditions in the bottom of sea ice during the Arctic spring, despite sufficient light being available for photosynthesis and the moderate accumulation of carbon biomass. These findings highlight the importance of (i) species composition on productive state, (ii) community respiration on net oxygen fluxes between the ice and ocean, and (iii) the potential influences of facultative heterotrophy or sustained ice colonization by pelagic cells throughout the bloom. The occurrence of a net heterotrophic state at a time when algae dominate the ice community also challenges the common assumption that photosynthesis during the spring bloom will always result in positive net production (autotrophy) [e.g., *Kaartokallio*, 2004]. Such assumptions are especially problematic if measurements of gross primary production are used to assess the contribution of sea ice algae to carbon cycling, as heterotrophy (negative production) cannot be quantified by the commonly used ^{14}C incubation method [*Williams*, 1993]. Instead, future studies should consider the influence of respiration in sea ice throughout the ice algal bloom to ensure accurate representations of productive state, for example, by using an oxygen optode system like the present study or under water eddy covariance techniques [*Glud et al*., 2014]. Carbon cycling in sea ice communities may be more complex than previously anticipated. Given the observed rapid reduction in sea ice over the past few decades, it is important to take a closer look at the function of microorganisms in Arctic ecosystems.

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